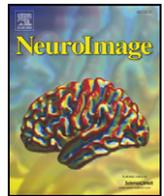




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Cerebral bases of subliminal speech priming

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ABSTRACT

While the neural correlates of unconscious perception and subliminal priming have been largely studied for visual stimuli, little is known about their counterparts in the auditory modality. Here we used a subliminal speech priming method in combination with fMRI to investigate which regions of the cerebral network for language can respond in the absence of awareness. Participants performed a lexical decision task on target items preceded by subliminal primes, which were either phonetically identical or different from the target. Moreover, the prime and target could be spoken by the same speaker or by two different speakers. Word repetition reduced the activity in the insula and in the left superior temporal gyrus. Although the priming effect on reaction times was independent of voice manipulation, neural repetition suppression was modulated by speaker change in the superior temporal gyrus while the insula showed voice-independent priming. These results provide neuroimaging evidence of subliminal priming for spoken words and inform us on the first, unconscious stages of speech perception.

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Introduction

There is now considerable evidence that neural activity in the visual cortex can occur in the absence of stimulus awareness (Dehaene et al., 2001; Rees et al., 2002). After almost a century of debate on the existence of unconscious perception, the last decade has been rich in demonstrations both of neural and behavioral effects induced by subliminal stimuli [see Kouider and Dehaene, 2007, for a review]. These demonstrations have primarily relied on the combined use of visual masking and priming to induce measurable subliminal influences: a highly visible target stimulus is processed more efficiently when preceded by a related masked prime than by an unrelated prime (Dehaene et al., 2001; Dehaene et al., 1998; Forster and Davis, 1984; Kouider and Dupoux, 2001; Marcel, 1983). While behavioral findings indicate that a masked word or digit can have an influence on sensory, perceptual, lexical, and, under some conditions, semantic levels of processing, neuroimaging methods directly visualize the brain activations that a subliminal prime evokes in several cortical areas [see Kouider and Dehaene, 2007].

However, although important advances have been made in the visual modality, how the human brain responds to subliminal auditory stimuli remains unknown. Several fMRI studies have shown that subliminal visual priming is associated with a reduced activity for repeated stimuli compared to unrepeated trials (the “repetition

suppression” phenomenon, see Henson, 2003) in posterior perceptual regions, notably the Visual Word Form Area (VWFA) for written words (Dehaene et al., 2001), and the Fusiform Face Area (FFA) for faces (Kouider et al., 2009). Whether auditory stimuli presented below the threshold of consciousness can similarly modulate cortical activity has not yet been examined.

In this study, we address this issue by using fMRI in combination with a subliminal speech priming paradigm (Kouider and Dupoux, 2005). Participants performed a lexical decision task on spoken word and pseudoword targets preceded by subliminal primes. Contrary to previous studies combining spoken word priming and fMRI through the use of supraliminal stimuli (Gagnepain et al., 2008; Orfanidou et al., 2006), here the primes were rendered subliminal by time compressing and embedding them within a stretch of speech-like noise, and presented just prior to the target stimuli (Fig. 1).

The use of subliminal processing is meant to characterize the initial stages of speech perception and their neural correlates while avoiding potential strategic and attentional changes elicited by awareness of the prime–target relation (Naccache and Dehaene, 2001). Indeed, because masking allows to focus on bottom–up activations of the neural code associated with the word stimuli, while presumably preventing the top–down re-entry of information (Dehaene et al., 2006; Lamme and Roelfsema, 2000), subliminal perception supposedly reflects information about the information encoded in a given brain area, without contamination by the distant global broadcasting that may occur when words cross the threshold of consciousness.

In the present study, the stimuli were spoken by a male and a female speaker. In some trials, the prime and target were uttered by the same speaker, while for other trials, the speaker’s voice changed.

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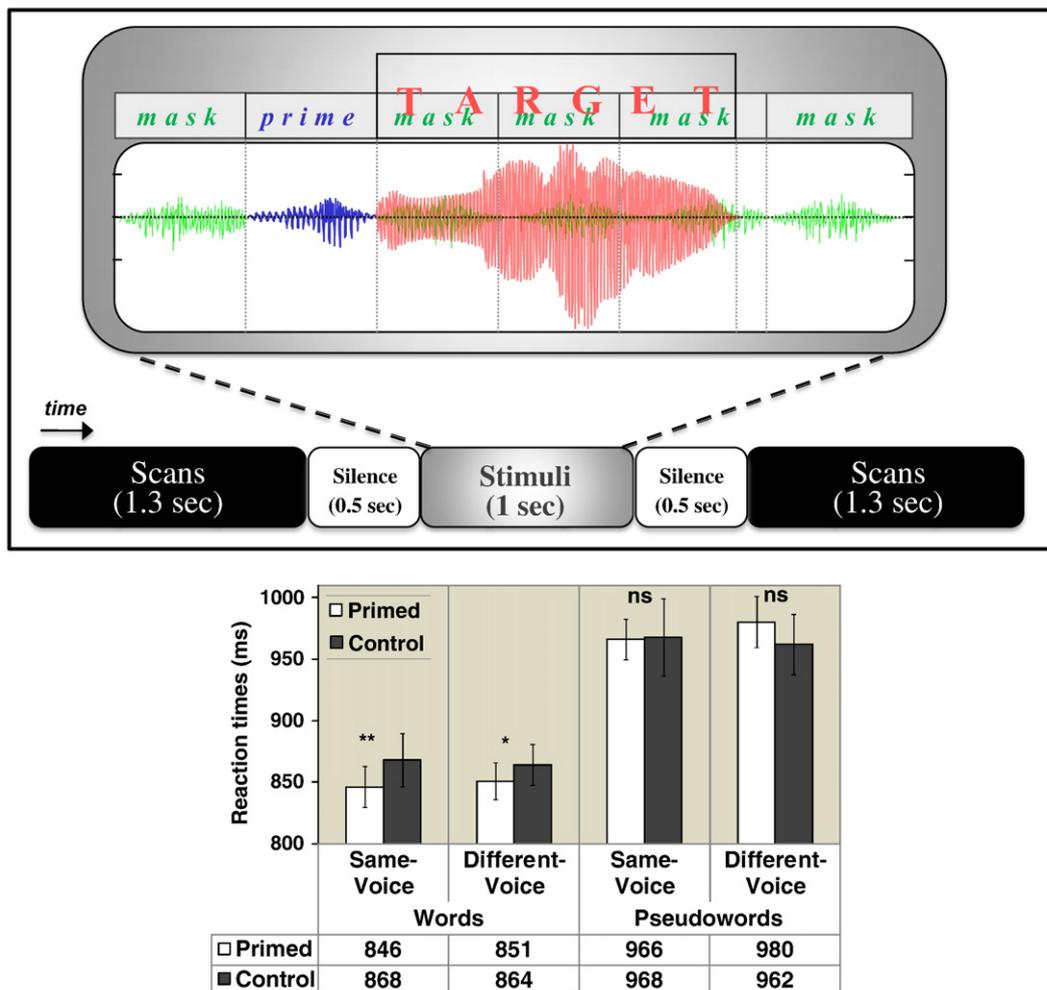


Fig. 1. Schematic description of the subliminal speech priming method (top panel) and behavioral results (bottom panel) representing the mean reaction times as a function of the prime–target relation (primed vs. control), the lexicity (word vs. pseudoword), and the voice relation (same vs. different voice).

By comparing repetition priming within and across voices, we aimed at dissecting the functional architecture of the spoken word recognition system (Grill-Spector and Malach, 2001; Naccache and Dehaene, 2001). More precisely, we expected regions performing speaker-voice normalization, that is the computation of an abstract phonetic code, to show voice-independent repetition suppression, for pseudowords as well as for words; regions performing lexical access were expected to show repetition suppression for words only; finally, regions encoding voice or speaker identity were expected to show voice-specific priming, independently of lexical status.

Materials and methods

Participants

A total of 16 right-handed French volunteers gave written consent to participate in the study (10 females, mean age 21.5 ± 2.2 years). All volunteers reported no hearing or language impairment and were in good health, with no history of neurological illness. The protocol of this study was approved by the regional ethical committee.

Stimuli and procedure

The material consisted of 224 pairs of auditory words and pseudowords (half CVC monosyllabic and half disyllabic CV–CV) recorded by both a male and a female talker. Within each pair, items

were matched in frequency of occurrence (for words), length, phonological (consonant–vowel) structure, but did not share any obvious formal or semantic relation. The pseudowords were all legal and pronounceable combinations of sounds in French. Each pair of items (X, Y) was used twice, once to create an unrelated control trial (prime $X \rightarrow$ target Y) and once to create a primed trial (prime $X \rightarrow$ target X) while ensuring that every participant received each target item only once during the whole priming experiment. Fig. 1 gives a description of the presentation procedure. The primes were time compressed to 35% of their original duration using the PSOLA algorithm, attenuated by 15 dB, and surrounded by one forward and four backward masks. Each mask received the same attenuation and resulted from the digital superposition of both a female and a male time-reversed compressed prime that were randomly selected. The target stimulus was presented at a normal rate and amplitude, right after the prime, overlapping with the backward masks. The subjective impression was that of a clear target surrounded by unintelligible babble noise (i.e., the same type of noise that arises from background conversation in a room; some stimuli can be heard at http://www.pallier.org/auditory_subliminal_priming). Participants were asked to perform a speeded lexical decision on the target and to ignore other auditory events. Reaction times were measured from the onset of the targets. In addition to the priming trials, participants received 20% of mask-only baseline trials consisting of the same sequence of events except that the prime and the target were absent (to ensure a timing similar to the priming trials, a random prime was selected and inserted

between the forward and backward masks, but finally played at a null volume). Participants did not perform any task during these trials.

The prime–target relation (repetition vs. control), prime voice (male vs. female voice), and target voice (male vs. female voice) were counterbalanced across items and participants by using a Latin square design. Half the participants responded word with the right hand and pseudoword with the left hand, and this assignment was reversed for the remaining participants. The priming experiment was divided into 4 blocks each consisting of 112 priming trials, 28 mask-only trials, and 4 initial trials that were later discarded (to eliminate nonequilibrium effects of magnetization in the scanner). The delay separating the onset of two trials corresponded to the 3.3 s TR of the fMRI sequence. Within each block, the voice of the target remained constant, while the voice of the prime and its relation to the target was mixed. Participants also received 30 additional trials for training purposes at the beginning of the experiment. The protocol was run using the E-prime presentation software (Psychology Software Tools; <http://www.pstnet.com>).

Measures of awareness

Following the priming experiment, half the participants were asked to perform a lexical decision on the primes, whereas the remaining participants performed a speech/nonspeech decision task on the primes (Kouider and Dupoux, 2005). During this period, although we did not analyze the imaging data, participants remained in the scanner and received the same EPI sequence to ensure that the acoustical conditions of the prime awareness phase did not differ from the masked priming phase. Half of the target stimuli were presented either under the same situation as in the priming experiment (with both primed and control trials from the priming conditions), and half were preceded by a prime with a different lexicality (for the lexical decision), or a backward-speech prime (for the speech decision). Participants were instructed that contrary to the priming experiment, they had to concentrate on the prime, ignoring the target and that only accuracy was important. They received 56 experimental trials, each one lasting two TRs of the fMRI sequence. The stimulus sequence was presented at the beginning of the first TR, and participants were instructed that they could take as long as 6 s to respond (i.e., before the end of the second TR). Care was taken to ensure that participants understood the task correctly. To do so, the experimental trials were preceded by 12 practice trials where the prime was amplified to the level of the target, a 100-ms silence was introduced before and after the prime, the masks were attenuated by an additional -5 dB, and visual feedback was provided to the participants.

fMRI procedure

We used a 3-T whole body system (Bruker, Germany) using a standard head coil optimized for a gradient echo–echo planar imaging sequence (25 contiguous axial slices, 3-mm thickness with 1-mm gap, TE = 40 ms, flip angle = 90° , field-of-view = 192×256 mm², 64×64 pixels). A clustered acquisition scheme was employed with a time of repetition of 3.3 s and a time of acquisition of 1.3 s. The stimulus sequence lasted about a second (mean duration = 1018 ms; SD = 30 ms) and was presented in the 2-s silent gaps between scans. The stimuli were played 500 ms after the end of the preceding scan. In addition, high-resolution T1 anatomical images ($1 \times 1 \times 1.2$ mm) were obtained at the beginning of the priming experiment.

Data analysis

The same basic analysis was performed on the imaging data and on the behavioral priming data with median correct response times. It consisted in a $2 \times 2 \times 2$ repeated-measures analyses of variance (ANOVA) with prime–target relation (primed vs. control) \times lexicality

(word vs. pseudoword) \times voice relation (same vs. different voice) as within-participant factors. The functional images were processed using the SPM2 software (Wellcome Department of Cognitive Neurology, London, UK). Four initial volumes were discarded to eliminate nonequilibrium effects of magnetization. Images were corrected for slice acquisition delays and motion, then, normalized into the MNI space using a nonlinear transform calculated from the anatomical image (2-mm voxel resampling) and finally spatially smoothed with an isotropic Gaussian filter (12-mm FWHM). The time series for each voxel was high-pass filtered at 1/128 Hz. Statistics were computed in two steps. First, a parameter estimate image for each of the event types was computed by fitting each voxel time series with a timecourse created by convolving delta functions at the onset of each target with a canonical hemodynamic response function (HRF). In the second step, group-based statistical inferences were made using a random effect model and performing the ANOVA mentioned above on the canonical HRF parameter estimate images of all participants with voxelwise $p < 0.001$ and a minimal cluster extent of 20 contiguous voxels.

Results

Behavioral results

Debriefing following the priming experiment but before the prime awareness test revealed that none of the participants noticed the presence of the prime stimuli, nor did they notice repetitions of the same word within a trial. The forced-choice judgment on the primes confirmed that participants could not identify them, as their performance did not differ significantly from the 50% chance level (51.1%; $t_{(15)} = 0.93$, $p = 0.37$). This was also true when considering the speech decision and lexical decision tasks separately (49.6% and 53.4%, respectively; both $p \geq 0.13$). Having established that the primes were subliminal in our study, we turned to the analysis of their influence on behavioral priming.

The average lexical decision times are shown on Fig. 1, bottom panel. An analysis of variance performed on these data, with the three within-participant factors, prime–target relation, lexicality, and voice relation, failed to reveal a significant global priming effect ($p = 0.16$) but showed a significant interaction between priming and lexicality [$F_{(1,15)} = 5.98$, $p < 0.05$]. This interaction was due to the fact that priming was significant for words [$F_{(1,15)} = 13.48$, $p < 0.005$], but not for pseudowords ($p = 0.31$). Restricted comparisons revealed significant word priming in the same-voice condition [$F_{(1,15)} = 10.57$, $p < 0.01$] as well as in the different-voice condition [$F_{(1,15)} = 4.56$, $p < 0.05$], without difference between them (priming by voice interaction: $p = 0.36$). Similar comparisons on pseudowords did not reveal any significant effect (all p values > 0.20). The behavioral data collected in this study thus replicate the priming pattern found in our previous behavioral study (Kouider and Dupoux, 2005), as well as that classically observed in subliminal visual priming: masked priming for words but not pseudowords (see, e.g., Forster and Davis, 1984). It is of note, however, that the magnitude of priming was about twice weaker in the present study, likely resulting from the fact that the acoustical conditions were degraded in the scanner.

Imaging results

We first looked at the neural activity associated with the auditory lexical decision task relative to the baseline mask-only trials (see Fig. 2). It involved a large network consisting of the left perisylvian regions (superior temporal gyrus [STG] including Heschl gyrus [HG], planum temporale and polare, inferior frontal gyrus, insula, supramarginal gyrus, inferior parietal lobule), the right HG and insula, the cuneus, cingulate and posterior medial frontal gyri, the hand motor cortices, and subcortical structures bilaterally

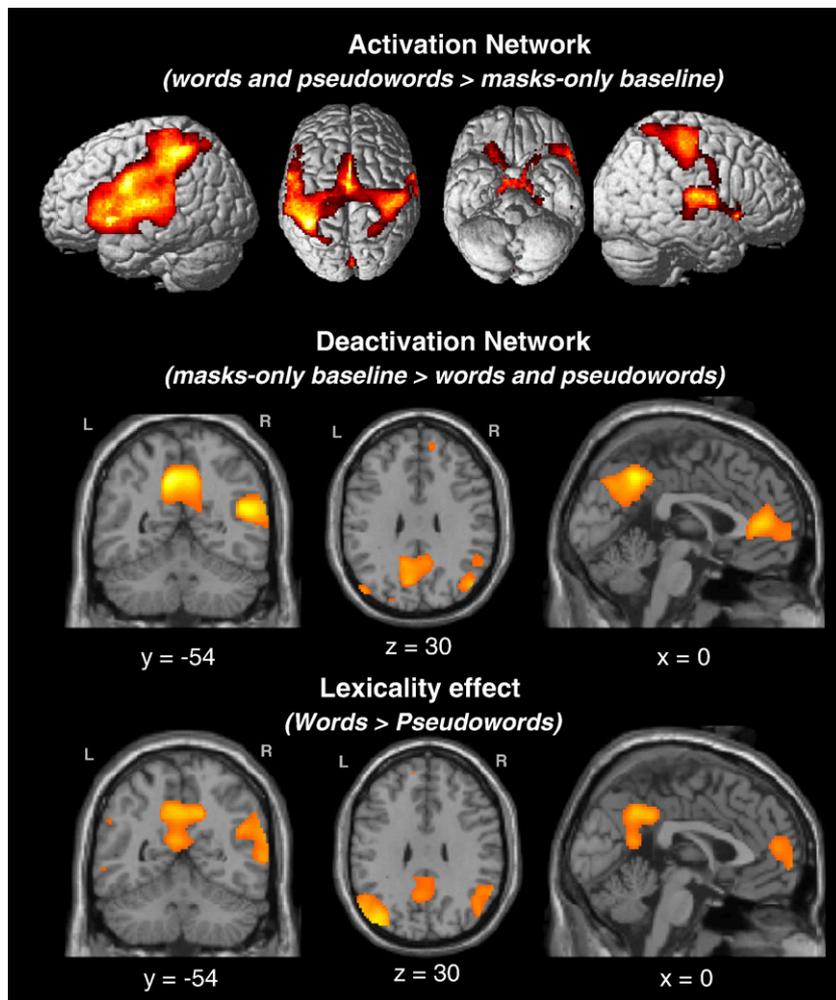


Fig. 2. Activation (top part) and deactivation (middle part) networks associated with the auditory lexical decision task and cerebral network associated with lexicality (bottom part). Note that the latter two networks are virtually identical. L = left hemisphere; R = right hemisphere. The coordinates below the images refer to the value at which slice were taken.

(thalamus, putamen, caudate nucleus). Conversely, the precuneus, the medial superior frontal gyrus, the anterior cingulate, and the right posterior STG were “deactivated” by the task. The network of regions showing greater activations for words compared to pseudowords was virtually identical to the “deactivation” network (see Fig. 2), showing that pseudowords actually provoked stronger “deactivations” than words in those regions. Activation for the inverse contrast (pseudowords greater than words) was observed only in the supplementary motor area.

We then searched for regions sensitive to priming (i.e., showing a difference between primed and control trials). We report hereafter the results for words and then for pseudowords. We first investigated global word priming (i.e., collapsed across same- and different-voice conditions) and found that it led to repetition suppression (i.e., a decrease in neural activity) in two clusters (Fig. 3, top part), one in the left HG/planum polare (72 voxels; Montreal Neurological Institute [MNI] coordinates: $-40, -18, 0; Z = 3.81$) and in the right mid-level insula (180 voxels; MNI: $38, 6, 6; Z = 4.21$). We then looked at the priming contrast restricted to trials where the prime and the target were pronounced by the same speaker. This analysis revealed activations in the same two areas: while the insula cluster in this contrast was virtually identical to the one for global priming, the left temporal cluster was now about three times larger (262 voxels), extending from planum temporale to the planum polare with its maxima on the Heschl gyrus (Fig. 3, bottom part). We then searched for regions showing a significant interaction between priming and voice change. This analysis revealed a voice-specific modulation of

activity in the posterior part of the left temporal cluster (see Fig. 3, bottom part). By contrast, the interaction between voice and priming was not significant in the right insula. The magnitudes of activations at the peak coordinate for the global word priming contrast) were 1.5 for the between voice and 1.1 for the different voice contrasts ($F < 1$). While no cluster reached significance with the $p < .001$ threshold for the contrast of word priming across voices, the right insula showed repetition suppression at a more lenient threshold of 0.005 ($Z = 2.81$). No regions showed “repetition enhancement” (i.e., an increase for the primed condition) for words in any of the analyses above.

In order to address the relationship between the behavioral and the neural repetition effects for words, we computed correlations between the individuals’ priming on reaction times and the neural repetition suppression effect at the peak voxels in the two clusters identified above. None of the correlations reached significance (in the right Insula, $r = 0.09; p = 0.71$; in the left temporal cluster, $r = 0.22, p = 0.41$). Finally for words, as concerns the laterality of the activations, it is noteworthy that using a more lenient voxel-level threshold of $p < 0.005$ for the contrast of global word priming, we also found a cluster in left insula ($Z = 2.74$; MNI coordinates: $-22, 6, 8$) with a similar repetition suppression pattern for priming within and across voices (interaction $F < 1$). However, no cluster was observed in the right temporal lobe even with a very lenient threshold of $p < 0.05$.

We then performed the same analyses on pseudowords, and we similarly found some brain regions showing repetition suppression but no region of repetition enhancement. The contrast of global pseudoword priming (i.e., collapsed across same- and different-voice

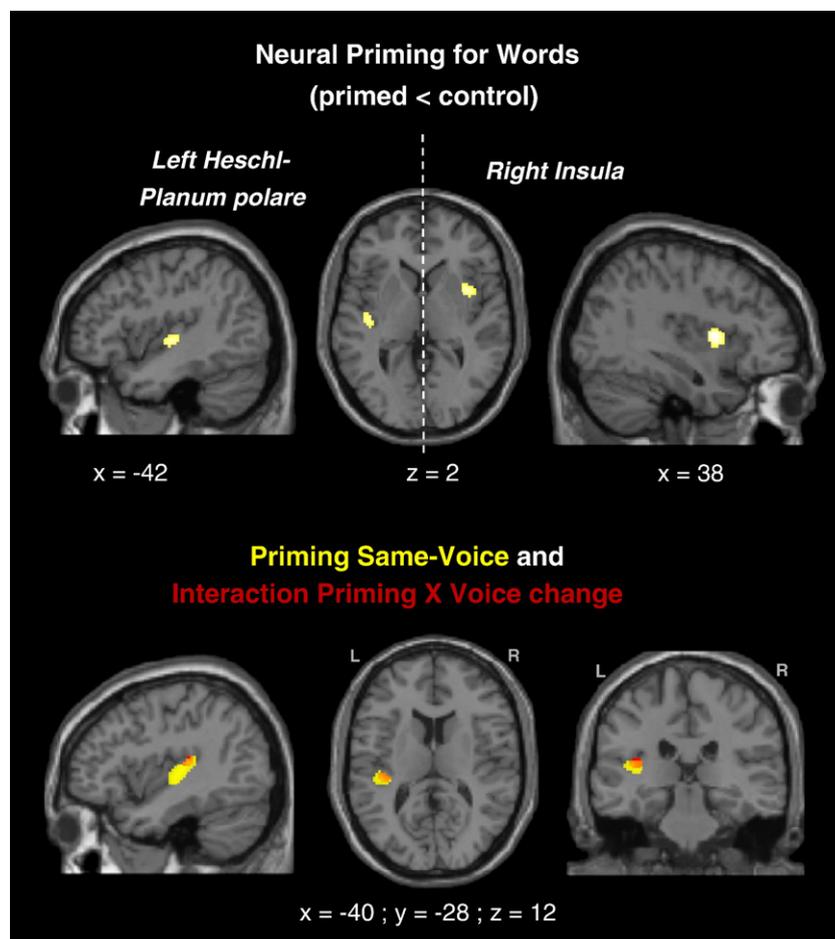


Fig. 3. (Top) Two regions showed repetition suppression for words: one in the left HG/planum temporal and the other in the right insula. (Bottom) Two overlapping clusters revealing word priming for trials in the same voice (in red) and an interaction between priming and voice change (in yellow).

conditions) revealed repetition suppression in the medial superior frontal gyrus (Fig. 4). As for the insula in the analysis of words above, the pattern of activation for this region was voice-independent, i.e., with similar amplitudes in the same- and different-voice conditions ($F < 1$). Importantly, the pattern of activation for this region was negative compared to the baseline. Given that this region also revealed a lexicality effect (see Fig. 2), repetition suppression here should rather be interpreted as an increased deactivation for repeated compared to unrelated trials (we come back to this aspect in the Discussion). The contrast of priming in the same voice revealed repetition suppression in the left caudate nucleus. Nevertheless, this region did not show up in the interaction between priming and voice change, rendering difficult to consider whether it is voice-specific or voice-independent. For the contrast of pseudoword priming across voices, again similarly to the insula above, the medial superior frontal gyrus showed up only at a more lenient threshold of 0.005 ($Z = 2.73$).

Finally, searching for regions showing interactions between priming and the other factors (i.e., lexicality and voice change), we found an unexpected three-way interaction in the left HG. As can be seen in the bottom part of Fig. 5, this complex interaction resulted from the fact that this left HG cluster was only sensitive to priming in the same voice, in the form of suppression for words ($p < 0.005$) and enhancement for pseudowords ($p < 0.05$).

Discussion

The present study aimed at investigating the neural correlates of subliminal speech priming. The behavioral results in this study

replicate the previous findings of Kouider & Dupoux (2005). Indeed, although the magnitude of priming on reaction times was about twice smaller here, we also observed a subliminal repetition priming effect for spoken words but not for pseudowords, and we also found that the amplitude of priming was not affected by whether or not the prime and target were spoken by the same speaker. This result shows that the behavioral priming effect in lexical decision task is voice-independent and suggests that it relies on the repetition of abstract phonetic or lexical representations (Luce and Lyons, 1998; Pallier et al., 2001).

At the cerebral level, we found that priming for words produced repetition suppression in the left superior temporal gyrus (planum polare, HG, and planum temporale) and in the mid-insula (see Fig. 3). Although behavioral priming reflected only voice-independent priming, fMRI data revealed that the left STG was sensitive to voice-specific priming. The amplitudes of repetition suppression in the insula or in the STG did not correlate with behavioral priming. Repetition suppression was also observed for pseudowords in the medial superior frontal gyrus and in the caudate nucleus. In the STG, we found that contrary to words, pseudoword priming led to response enhancement rather than suppression.

Voice-independent priming

We expected to find voice-independent repetition suppression in temporal regions performing phonetic decoding and word recognition but the only area where we observed voice-independent priming for words is the right insula (and we found a similar, although less statistically robust, pattern in the left insula). It is notable that Orfanidou et al. (2006) using priming with supraliminal primes also

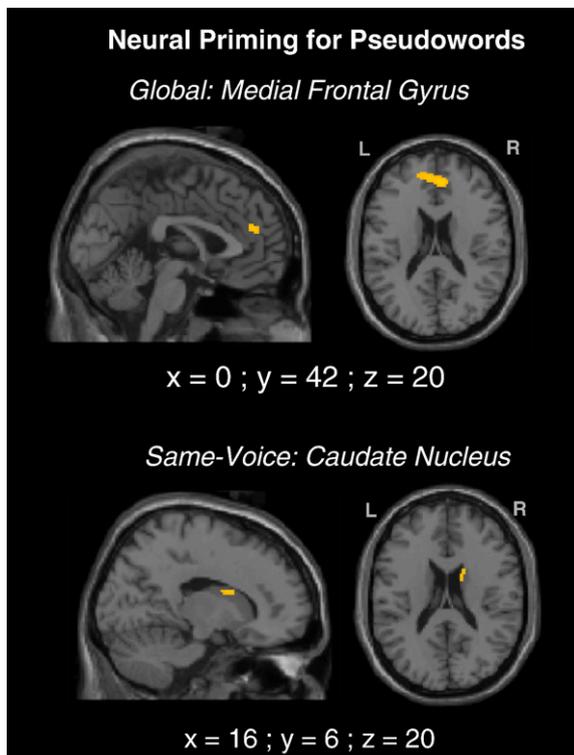


Fig. 4. Two regions revealed repetition enhancement for pseudowords: the middle frontal gyrus (for trials collapsed across voice change) and the caudate nucleus for trials in the same voice.

reported repetition suppression in the right insula. The insular cortex is often considered to be involved in speech output processes, particularly articulatory planning (Dronkers, 1996; Hickok and Poeppel, 2007). However, both clinical and neuroimaging evidence indicate that both left and right insulae are also involved in auditory processing (Bamiou et al., 2003; Bamiou et al., 2006; Engelen et al., 1995; Sander et al., 2005). Bamiou et al. (2003) remarked that some patients with spared HG but strokes involving the insulae had prominent auditory deficits. A recent study using electrophysiological recordings in macaque monkeys reported highly selective responses to vocalizations in the insula (Remedios et al., 2009), which led the authors to propose that the insula is part of a processing stream involved in the representation of communication sounds. One may also argue that the insula is part of a network processing the emotional aspects of sounds (Campanella and Belin, 2007; Sander et al., 2005).

Although the insula seems to be involved in some aspects of auditory/speech processing, we do not believe that speaker normalization, that is the computation of an abstract phonetic representation, is achieved by the insula itself. The most compelling argument comes from data on Broca's aphasics having damaged insula but spared word recognition capabilities, demonstrating that the insula is not essential for lexical access (Moineau et al., 2005). It seems therefore more likely that the sensitivity of the insula to lexical priming reflects information received from temporal regions that perform phonetic computations. It has been noticed by Downar et al. (2000) that the right insula was responsive to immediate changes regardless of whether the stimulus was in the visual, tactile, or auditory (nonspeech) modalities. These authors proposed that the insula belongs to a network for the automatic detection of changes in the sensory environment. Our finding that the insula is sensitive to subliminal primes adds new evidence in favor of this theory. Contrary to previous studies using supraliminal stimuli, here, participants were not consciously aware of the change. Our results support the automatic nature of the insula's reaction to change. It has been

suggested that the anterior insula is an important hub systematically associated with conscious experience (Craig, 2009). The present results should at least serve to qualify this conclusion by showing that a rather anterior insular area ($y = +6$ mm) can be modulated subliminally.

Voice-specific priming

A region showing voice-specific repetition suppression must encode the stimuli in a form that retains information both about the speaker and the phonetic content. This is the case, for example, of a detailed acoustic representation. Inasmuch as the prime and target are acoustically more similar when spoken by the same speaker, it is tempting to interpret the sensitivity of repetition suppression to voice change in the HG/STG as showing that these regions encode the stimuli's acoustic properties. This is precisely the conclusion of a study using an oddball paradigm (Celsis et al., 1999), where the authors observed a recovery from adaptation in BOLD signals from the posterior STG for both speech and nonspeech stimuli (tones) and concluded that this region is implicated in the preattentive detection of acoustic changes (see also Joanisse et al., 2007). HG and the adjacent parts of the dorsal STG are typically activated as strongly by speech as by acoustically matched nonspeech stimuli (see, e.g., Dehaene-Lambertz et al., 2005; Obleser et al., 2007; Rimol et al., 2005).

However, this does not imply that activations in the dorsal superior temporal gyrus merely encode acoustical/auditory properties of auditory stimuli. For instance, Jacquemot et al. (2003), comparing French and Japanese speakers listening to identical stimuli, found that activations in the left HG/planum temporale were influenced by the language of the participant; more precisely, language-specific phonological changes produced a stronger recovery from adaptation in an odd-ball paradigm than did nonphonological acoustic changes. This suggests that processing in the HG/STG may be influenced by linguistic experience. It is difficult to know, however, if the activations observed by Jacquemot et al. reflected top-down

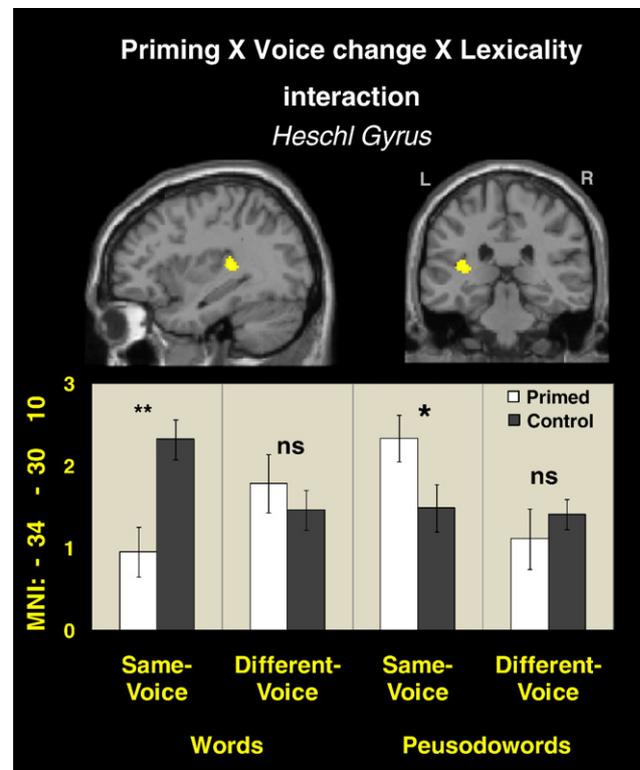


Fig. 5. Three-way interaction in the left HG reflecting the fact that this region is voice-specific and results in suppression for words but enhancement for pseudowords.

influences resulting from conscious processing of the stimuli, or rather on local computations performed during the initial stage of speech perception (see below).

The current data go one step further by showing a lexicality effect in the dorsal STG in the form of response suppression for words and response enhancement for pseudowords (Fig. 5).

Exactly the same effect (repetition suppression for words and repetition enhancement for pseudowords) was reported in the same region in a recent long-term priming study (Gagnepain et al., 2008). Beyond the replication with subliminal primes in an immediate repetition priming situation, we also find that voice change modulated these effects. There are two potential interpretations for this lexical effect, a first one referring to a bottom-up and early selectivity of priming as a function of the lexical status of the stimuli, and a second one to a top-down and late modulation of priming.

According to the first interpretation, the primes are processed automatically in a bottom-up fashion but have different subsequent impacts on the target as a function of lexical status. In this context, the HG would be sensitive to lexical factors because the neural representations stored in this region are already selective for words compared to pseudowords. This interpretation is compatible with exemplar-based models of word recognition (Goldinger, 1998; Pisoni, 1997). According to such theories, word forms are stored as multiple memory traces encoding many nonphonetic details of each encounter with a given word, including information about the speaker who produced the word. Such a model predicts that a word can be recognized more efficiently when it has already been heard produced by the same speaker. If the STG/HG stores lexical exemplars, then this could explain differential effects of repetition priming for words and pseudowords. It must be stressed, however, that the reaction-time data, being insensitive to voice manipulations, are not compatible with a pure exemplar-based model of the lexicon but can be explained in the recent hybrid model proposed by Goldinger (2007). In this revised model, along with episodic and acoustically detailed representations, abstract phonetic representations are also computed automatically in speech perception (see also Pisoni and Levi, 2007).

Yet, an account in terms of early lexical selectivity would a priori predict lower or even null priming for pseudowords compared to words, while we actually found an opposite pattern of results. Thus, although we cannot fully rule it out, this bottom-up hypothesis is rather unlikely. According to us, the second type of interpretation in terms of top-down modulation is more compatible with an inversion of priming as a function of stimuli's lexical status. Previous studies using supraliminal stimuli have shown that the direction of priming might shift from suppression to enhancement as a function of familiarity, with unfamiliar items leading to enhancement (Henson et al., 2000) and perceptual difficulty, with degraded stimuli leading to enhancement (Turk-Browne et al., 2006). It is possible that the modulation obtained here similarly reflects higher difficulty with the unfamiliar pseudowords, even under subliminal conditions of prime processing. Although masked priming has traditionally been associated with automatic, bottom-up processing (Forster, 1998), more recent studies show that it can actually be modulated by task-specific factors even if the prime stimuli are subliminal. Indeed Nakamura et al., using TMS (Nakamura et al., 2006) and fMRI (Nakamura et al., 2007) have shown that the brain circuitry involved in repetition priming for visual words differs as a function of task-specific mechanisms. That is, subliminal repetition priming for the same stimuli either engaged dorsal pathways in a naming task or ventral pathways in semantic or lexical decision tasks. Of particular relevance here is the fact that not only the brain circuitry for subliminal word priming differed as a function of task but also its direction: while the semantic decision led to repetition suppression, the naming task induced repetition enhancement for the same word stimuli (Nakamura et al., 2007). In addition, analysis of effective connectivity

revealed that enhancement in the naming task, but not suppression in the semantic decision task, was associated with backward projections (from articulatory/motoric systems to perceptual areas). These backward projections and the reversal of suppression into enhancement were interpreted as reflecting self-monitoring and feedback regulation (Nakamura et al., 2007). It is possible in our study that pseudoword targets similarly recruited additional feedback mechanisms resulting in repetition enhancement. Although the reasons for these changes in the directions of priming still remain unclear and require further investigations, the present study suggests that subliminal processing can be modulated in a top-down fashion not only by task manipulations but also by as a function of the familiarity/lexicality of the stimuli.

Additional priming modulations for pseudowords

Two other regions revealed repetition suppression for pseudowords, namely, the caudate nucleus and the medial superior frontal gyrus. The priming effect found in the caudate nucleus in this study is congruent with the finding, from both fMRI and clinical investigations in Huntington disease patients, that this region is directly implicated in the motor inhibition of subliminal primes (i.e., incongruent visual arrows) (Aron et al., 2003). The medial superior frontal gyrus may reflect inhibitory processes associated with the difficulty of rejecting (i.e., saying “no” to) pseudowords in repetition trials. As explained above (see the Results section), the priming modulation for pseudowords in medial superior frontal gyrus should rather be interpreted as an increased deactivation for repeated compared to unrelated trials. In addition, this region has been implicated with perceptual decision making in several studies, on the basis that the BOLD response is enhanced during difficult compared to easy trials (see Heekeren et al., 2008, for a review).

In sum, this study demonstrates the feasibility of subliminal auditory priming in fMRI despite the relatively degraded acoustic conditions in the scanner. Here, we have employed this technique to identify early processing stages of lexical access. More work could be done in this domain by investigating higher levels of processing, for instance, by comparing the effect of phonological and semantic priming. Masked auditory priming, combined with fMRI, could also be a valuable tool to investigate the processing of nonlinguistic auditory stimuli and assess if different dimensions of sounds (e.g., pitch, timbre) lead to dissociable patterns of repetition suppression in specific areas.

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